TRANSPORT OF DUNGENESS CRAB (*CANCER MAGISTER*) MEGALOPAE INTO GLACIER BAY, ALASKA

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ABSTRACT

Areas of high *Cancer magister* larval recruitment and transport mechanisms were identified in the lower portion of Glacier Bay, Alaska. Megalopae were collected at three sites in 2004 and 2005 using light traps positioned within 1 m of the surface and bottom at 10 m depth. Surface traps captured 96.5 – 99.4 % of megalopae collected. Megalopae abundances were highly pulsed and decreased with increasing distance from the mouth of Glacier Bay. Spatial variation was similar between years with significant differences among all sites in 2005. Half of the total annual megalopae supply occurred over just two nights in September or October, the dates of which varied by location. Megalopae abundance in Bartlett Cove was negatively cross-correlated with tidal amplitude at -3 to +1 d lags and positively cross-correlated with maximum wind speed at a 0 d lag. Megalopae abundance in the South Beardslee Islands was positively correlated with tidal amplitude and negatively correlated with maximum wind speed at +2 to +3 d lags. Abundance in the North Beardslee Islands was low and not correlated with tides or winds. Spatial variation in megalopae abundance and correlations between abundances and transport processes suggests that Dungeness crab megalopae are transported into Glacier Bay.

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INTRODUCTION

Identification of areas with high Dungeness crab (*Cancer magister*) larval recruitment may benefit fisheries as the distribution of early life stages has been shown to affect spatial and temporal variations in adult populations (Botsford et al. 1989, Botsford et al. 1998, Botsford 2001, Botsford & Lawrence 2002, Shanks & Roegner 2005). Knowledge of such areas with high larval or juvenile abundances may also be an asset in the design of new marine reserves, making it possible to include these critical life stages within reserve boundaries (Jones 2002, Roberts et al. 2003a, b, Botsford et al. 2003). However, mechanisms leading to spatial variation in larval supply are often difficult to determine, because larval behavior and hydrodynamic processes can interact in complex ways that prohibit generalizations (Shanks 1995, Epifanio & Garvine 2001, Quieroga & Blanton 2005). Spatial variation in larval supply is the result of complex biological and physical processes (Sale & Kritzer 2003) including (1) demographic rates (i.e. mortality; McConaugha 1992), (2) location and timing of larvae release (Forward 1987a, Morgan & Christy 1995), (3) pelagic duration (Roberts 1997, Shanks & Eckert 2005), (4) larval behaviors and sensory abilities (Sulkin 1984, Kingsford et al. 2002), and (5) hydrodynamic processes affecting larval transport (Wing et al. 1998, Etherington & Eggleston 2000). Long term studies of Dungeness crab recruitment in northern California suggest that spatial variation in larval abundance at relatively small scales (1-10 km) is most influenced by oceanographic processes affecting larval transport (Botsford et al. 1989, Botsford et al. 1998). Here, we examine spatial variation in

Dungeness crab megalopae supply in the context of larval transport processes among sites separated by 4-12 km in Glacier Bay, a marine reserve.

Early life history of Dungeness crabs

The Dungeness crab is a commercially important species found along the Pacific coast of North America from the Pribilof Islands, Alaska to Baja, Mexico (Jensen & Armstrong 1987). The behavior of adult and larval Dungeness crabs along the coast of the contiguous United States facilitates large-scale larval migration away from and then back to estuarine and nearshore areas (Lough 1976, Reilly 1983). The larvae have a long pelagic larval duration which increases at colder temperatures (Reed 1969, Sulkin & McKeen 1989, 1996). Estimates of larval duration range from 105 to 125 days in central California (Reilly 1983) to approximately 120-130 days on the outer coasts of Washington and Oregon (Lough 1976, Dinnel et al. 1993) to 145-160 days in Alaska (Shirley et al. 1987, Fisher 2006). *Cancer magister* larvae are found at progressively farther distances from shore with each larval stage (McConaugha 1988, Lough 1976, Reilly 1983, Jamieson & Phillips 1988, Jamieson et al. 1989). Megalopae in early intermolt have been observed beyond the edge of the continental shelf, up to 170 km off the coasts of Washington and Vancouver Island (Jamieson et al. 1989) and 185 km off the coast of California (Reilly 1983), but these larvae must return to shore for settlement, which, near Grays Harbor, Washington, occurs no further than 15 km offshore (Carrasco et al 1985, McConnaughey et al. 1992). Increasing abundances of megalopae in late intermolt have been found progressively closer to the coast of Vancouver Island, BC (Jamieson & Phillips

1988). Shoreward transport of Dungeness crab megalopae has been related to various physical parameters including lunar phase (Eggleston & Armstrong 1995), tidal cycle (Eggleston et al. 1998, Johnson & Shanks 2002, Miller & Shanks 2004) and wind events (McConnaughey et al. 1992, Jamieson & Phillips 1993, Eggleston & Armstrong 1995, Miller & Shanks 2004).

Larval transport patterns along the U.S. Pacific coast may not apply in Alaska because of differences in oceanic regime and coastline geography. Off the coast of Vancouver Island, the eastward-flowing Subarctic Current impinges on North America and bifurcates into the southward-flowing California Current and the northward-flowing Alaska Current (Sverdrup et al. 1942). The California Current regime can be characterized by upwelling and relaxation events (Huyer 1983). Off-shore larval migrations in the California Current system are directed first by upwelling-winds which move surface water and larvae away from the coast, and second by relaxation events at which time larvae return to the coast (Shanks et al. 2000). The Alaska Current regime is downwelling year-round (Royer 1998, Weingartner 2005, Weingartner et al. 2005). Larvae may thereby be concentrated in bottom waters at the edge of the narrow continental shelf in the Gulf of Alaska; however, the potential effects of oceanographic processes on larval transport are poorly understood in this region. Coastal Alaska is a highly complicated matrix of islands, bays, fjords and inlets that can not be compared with the relatively straight coastlines of Washington, Oregon and California, which are punctuated by few major bays and inlets. The most comparable area to the inside waters of southeast Alaska

along the coastline of Washington, Oregon and California is Puget Sound and the Georgia-Rosario Strait complex, which is a retention zone for Dungeness crab larvae (Jamieson & Armstrong 1991).

Dungeness crabs in Glacier Bay

Glacier Bay is the largest (1255 km^2) functional marine reserve for Dungeness crabs throughout their range. Glacier Bay is located 50 km from the Gulf of Alaska (GOA) and connected to the GOA through Icy Strait and Cross Sound (58° 24'N, 136° 00'W; Fig.1). Cross Sound narrowly opens to the GOA at a canyon that slopes downward and outward through the narrow coastal shelf (35 km wide) to the shelf break. Glacier Bay is a Y-shaped and recently deglaciated (< 300 years ago) fjord stretching approximately 100 km from north to south. It is surrounded by mountainous terrain with many freshwater sources including 10 tidewater glaciers in the upper bay. Glacier Bay is a highly dynamic area experiencing large amounts of freshwater runoff, high sedimentation and large semi-diurnal tidal variations. Average tidal amplitudes in Bartlett Cove are 3.7 m and can be as large as 7.3 m (Hooge et al. 2000, Hooge & Hooge 2002).

Commercial fishing of Dungeness crabs in Glacier Bay was closed by U.S. Congress in 1998 (Department of the Interior 1998). Dungeness crab studies in Alaska have primarily focused on the Glacier Bay population (Shirley & Shirley 1988, Leder et al. 1995, O'Clair et al. 1995, O'Clair et al. 1996, Schultz et al. 1996, Shirley & Taggart 1996, Shirley et al. 1996, Swiney et al. 2003, Taggart et al. 2003,

Taggart et al. 2004 a, b, Fisher 2006); however even the Glacier Bay population is not nearly as well understood as those in California, Oregon and Washington. The Multi-

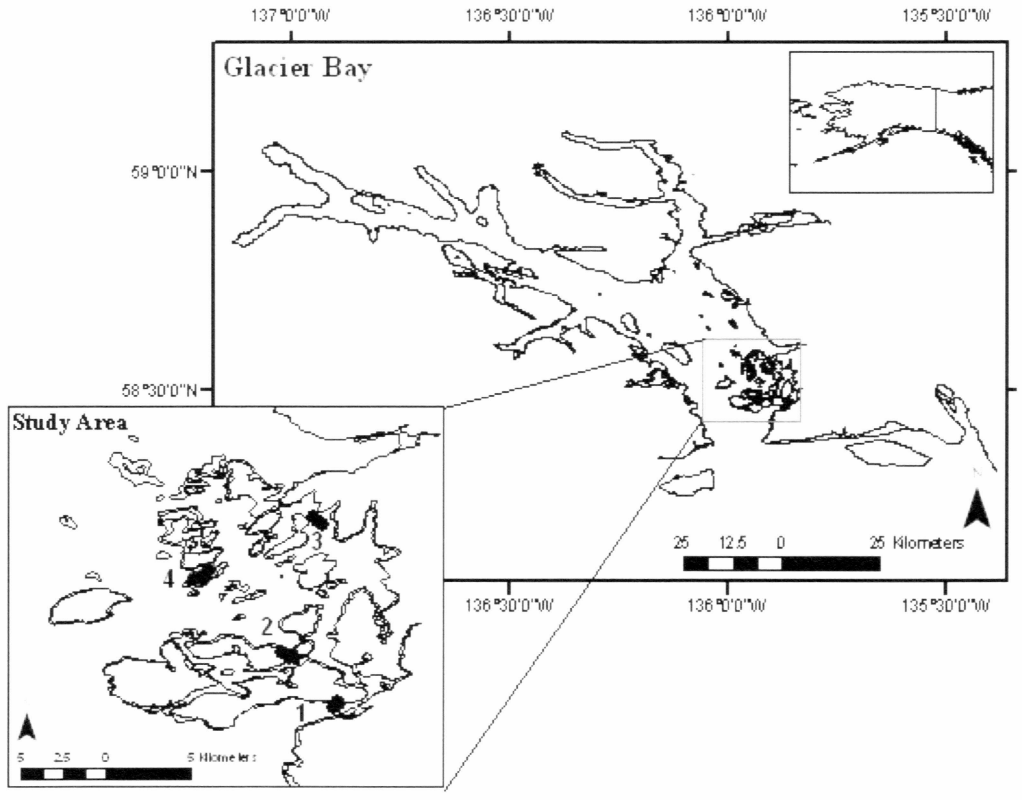

Fig. 1. Glacier Bay National Park, Alaska (58° 24'N, 136° 00'W) and detail of sampling locations within the lower bay indicated numerically: 1) Bartlett Cove, 2) South Beardslee Islands, 3) North Beardslee Islands (inside), and 4) North Beardslee Islands (outside). Dots represent replicate light trap locations. Note scale bars.

Agency Dungeness crab Survey (MADS), comprised of the U.S. Geological Survey (USGS), the University of Alaska Fairbanks (UAF), and the National Marine Fisheries Service (NMFS) has studied the size, behavior and abundance of adult Dungeness crabs at six sites in Glacier Bay with semiannual surveys each year from 1992 to 1997 and annual surveys thereafter (Taggart 2004 a, b). These sites are in the lower 40 km of Glacier Bay where 88% of all adult Dungeness crabs are found

(Taggart et al. 2003). No abiotic factor was determined that might be limiting to adult populations in the upper portion of the bay where adult crabs are rare.

A recent study in Glacier Bay (Fisher 2005) has examined the abundance of *C. magister* larvae in Sitakaday Narrows, Glacier Bay. In April - June, stages I and II *C. magister* zoeae were captured in plankton tows in average densities of 15-25 larvae/100 m^3, and sampling in July and August captured few later zoeal stages in plankton tows of Sitakaday Narrows (Fisher 2005). In comparison, high mean densities (600-1100 larvae/100 m^3) of the congener *Cancer oregonensis* were captured in plankton tows through August and included larvae up to stage 4 (Fisher 2005). Although *C. magister* larvae have not been widely observed in Glacier Bay in stages 2-5, high abundances of megalopae have been captured with light traps in Bartlett Cove (G. Eckert personal communication). The high abundance of all larval stages of *C. oregonensis* and the presence of only early zoeae and late-stage megalopae of *C. magister* suggests that *C. magister* larvae may be exported out of Glacier Bay while *C. oregonensis* larvae may be retained.

Pulses of *C. magister* megalopae in Bartlett Cove occur predominately from half to new moons in September and October (Douglas et al. 2003). The pulsed nature of megalopae abundances in Bartlett Cove suggests that *C. magister* megalopae may be transported into Bartlett Cove by hydrodynamic processes as has been shown in estuaries along the US Pacific coast (Jamieson & Phillips 1993, Eggleston & Armstrong 1995, Eggleston et al. 1998, Johnson & Shanks 2002, Miller & Shanks 2004).

In this study, we identify Bartlett Cove as an area of high larval recruitment for Dungeness crabs within Glacier Bay. Spatial variation in megalopae supply was substantial among locations sampled and varied similarly among locations in 2004 and 2005. For locations with substantial megalopae supply, pulses in megalopae abundance were cross-correlated with physical parameters (e.g. tidal amplitude and maximum wind speed), supporting the idea that megalopae are being transported into Glacier Bay just prior to settlement. We discuss the implications of larval transport into Glacier Bay on the sustainability of this marine reserve, an idea which has previously been addressed only in theory (Botsford et al. 1998, Botsford et al. 2001, Gaines et al. 2003, Hastings & Botsford 2006).

METHODS

Light traps

Light traps have been used to study brachyuran crab larvae and transport processes (Reyns & Sponagule 1999, Johnson & Shanks 2002, Roegner et al. 2003, Miller & Shanks 2004). Light traps are self-sufficient, simple, inexpensive, can sample over an extended duration, and most importantly, successfully catch crab megalopae, which are good swimmers and can avoid plankton nets (Natunewicz & Epifanio 2001, Jones & Epifanio 2005, Porter et al. in review). The light traps used in this study were modified from the design used by Roegner et al. (2003). Translucent 20 l rectangular containers made of plastic were fitted on each side with transparent funnels which tapered from 100 to 10 mm diameter. The bottom of the trap was capped with a removable PVC tube with 250 μm mesh at the cod end. As

traps were lifted from the ocean the water inside was expelled through the mesh, concentrating the sample in the cod end for collection. Bottom weights and foam floats ensured that the trap remained upright in the water column. Two Princeton Tec Attitude dive lights (total 6 LED lights per trap) were affixed inside each trap and continually illuminated. Batteries in the lights were changed every second day to ensure consistent light levels.

Sampling regime

Samples were collected in Bartlett Cove, the South Beardslee Islands and the North Beardslee Islands, along a gradient with increasing distance from the mouth of Glacier Bay (Fig. 1). Sites were separated by distances ranging from approximately 4 to 12 km. Three mooring lines were stationed at each of these sites, each line with two light traps, one each within 1 m of the top and bottom of the water column. Locations for mooring lines were selected randomly from MADS adult crab monitoring sites at 10 m depth MLLW (Taggart et al. 2004 a, b). Each surface trap was suspended by a buoy and the bottom trap fixed by an anchor so that traps remained in their respective positions throughout tidal cycles.

In 2004, surface and bottom traps in Bartlett Cove were sampled on a daily basis from September 11 to October 23. Sampling prior to September 16 was not possible in the Beardslee Islands because the area is closed by the National Park Service to motorized vessel traffic from May 1 to September 15. Sites in the Beardslee Islands were sampled on 12 days between September 19 and October 19 in 2004 (see Appendix for dates). In 2005, surface traps were sampled each day at all

sites from September 17 to October 31 with bottom traps sampled on a subset of these days (Appendix). An additional site on the outside of the North Beardslee Islands (Fig. 1) was added in 2005 to determine whether megalopae abundances were similar inside and outside the complex island archipelago which might restrict water flow. Three light traps were positioned at the outside North Beardslee site within 1 m of the surface at approximately 120 m intervals along the 10 m MLLW contour line for sampling.

Fish and other macroscopic, non-decapod organisms captured in light traps were identified, recorded and released at time of sampling. The remainder of the sample was preserved in 80% ethanol for lab processing in which brachyuran larvae were identified according to Lough (1974) and Shanks (2001) and enumerated. All Cancrid and commercially valuable crabs were identified to species and larval stage. Larvae of other crabs were identified to family (Grapsidae, Xanthidae, Pinnotheridae, Paguridae, and Majidae).

Physical data

Tide predictions for Bartlett Cove were generated by the XTide program found at http://tbone.biol.sc.edu/tide/sitesel.html (last accessed 1/2006). Tidal amplitudes were estimated by subtracting the lowest low tide from the highest high tide from noon of the previous day to noon of the sampling day. Residuals of Autoregressive Integrated Moving Averages (ARIMA) were calculated by subtracting the mean daily tidal amplitude over the sampling period from daily values. Hourly wind speed and directional data to the nearest 10 degrees were collected in Gustavus,

AK by the U.S. Department of Commerce National Climatic Data Center at station 703670 (58.41°N, 135.70 ° W) (http://cdo.ncdc.noaa.gov/pls/plclimprod/cdomain.abbrev2id; last accessed 9/2006). Daily wind speed maxima were calculated over the sampling period for pooled wind data and for data separated by major cardinal direction. ARIMA residuals for maximum wind speed were calculated by subtracting the mean maximum daily wind speed over the sampling period from daily values for both pooled and directionally stratified data.

Statistical analysis

Data were analyzed with SAS statistical software (v.9.1). Only samples collected on simultaneous days for all locations were used in analyses. Daily abundances of *C. magister* megalopae in each light trap were transformed by $\log_{10}$ (abundance + 0.1) to reduce and normalize variance among daily abundances. Transformed megalopae abundances in surface traps were compared with a two-way fixed-factor general linear model (GLM) and Tukey-Kramer post-hoc tests on least squared means for effects of year and location. Only surface samples were analyzed with year as an effect (surface n 2004/2005: Bartlett Cove 45/144, South Beardslee Islands 29/144, North Beardslee Islands 29/144). In analysis of depth effects, years were pooled and only days when all sites (except September 17, 18, 21 and October 1, 2 of 2004 when only two sites were sampled; see Appendix) were sampled at the surface and bottom were included (n surface/bottom: Bartlett Cove 93/78 South Beardslee Islands 77/68, North Beardslee Islands 77/67). A repeated measures GLM

was conducted to compare mean daily megalopae abundances among locations in 2005 because of non-independence of consecutive samples collected from the same light traps. Mean abundances of megalopae at the surface in the inside and outside North Beardslee Islands in 2005 were compared with a 1-tailed t-test for samples with equal variances in 2005 (North Beardslee Islands inside/outside: 90/90). Megalopae abundances in surface and bottom traps were compared with a two-way fixed factor GLM and Tukey-Kramer post-hoc tests for effects of location and depth for the subset of days when bottom traps were sampled. Estimates of interannual variation in Bartlett Cove were calculated by summing the total number of megalopae captured in surface traps over the 30 days of highest megalopae abundance for each 2004 and 2005.

Cross-correlation analysis

Procedures for ARIMA analyses followed those described by Johnson & Shanks (2002) and Miller & Shanks (2004). Residuals from tidal amplitude and maximum wind speed analyses were cross-correlated with residuals from 2005 megalopae abundances as an indicator of transport mechanisms. Because megalopae recruitment is seasonal and periodic, autocorrelation occurs in this type of time-series data set. To account for autocorrelation, data were pre-whitened using ARIMA procedures (Bence 1995, Pyper & Peterman 1998). The seasonal trend was removed by subtracting a 17-day moving average from the 2005 time series at each site. This length of moving average was chosen to achieve a minimum sum of squared residuals. Residuals from megalopae abundances were autocorrelated within each site

and cross-correlated with residuals from physical data. Cross-correlation analyses were only considered valid for lags < 10% of the length of the time series (Emery & Thomson 1997). Residuals of megalopae abundance were compared with residuals of tidal amplitudes at lags of -5 to +5 days. Cross-correlations with maximum wind speeds were only compared for positive lags (0 to +5 d) as effects of wind speed on previous megalopae abundances would be nonsensical. Correlation analyses must always be treated with caution as nonsensical correlations may occur (e.g. Love & Westphal 1981).

RESULTS

Spatial variation

Patterns of spatial variation in megalopae abundance in surface traps were the same in 2004 and 2005, with the highest megalopae abundance in Bartlett Cove, followed by the South Beardslee Islands, and then the North Beardslee Islands (Fig. 2; Table 1). Differences in megalopae abundance among sites were highly significant in 2005 but were not significant in 2004, likely because of small sample size since the trend was similar to that of 2005 (Fig. 2; Table 2). Few megalopae were caught in surface traps at the inside or outside North Beardslee Islands, and megalopae abundances were not significantly different between those two sites (1-tailed t-test: df = 178; $p = 0.298$; Fig. 3). Hereafter, all references to the North Beardslee Islands site refer to the inside North Beardslee Islands location. Repeated measures analysis for the 2005 sampling season resulted in significant variation among surface megalopae

abundances among Bartlett Cove, the South Beardslee Islands and the North Beardslee Islands (df = 2; F = 47.67; MS = 63.28; p = 0.0002).

Table 1. Summary of two-way GLM with effects year (2004 or 2005) and location (Bartlett Cove, South Beardslee Islands or North Beardslsee Islands) upon log transformed daily *Cancer magister* megalopae abundance at the surface.

Source of variation	df	MS	F	Probability
Year (fixed factor)	1	31.57	43.09	< 0.0001
Location (fixed factor)	2	71.05	96.98	< 0.0001
Year x Location	2	1.29	1.76	0.2091
Error	529	0.74		

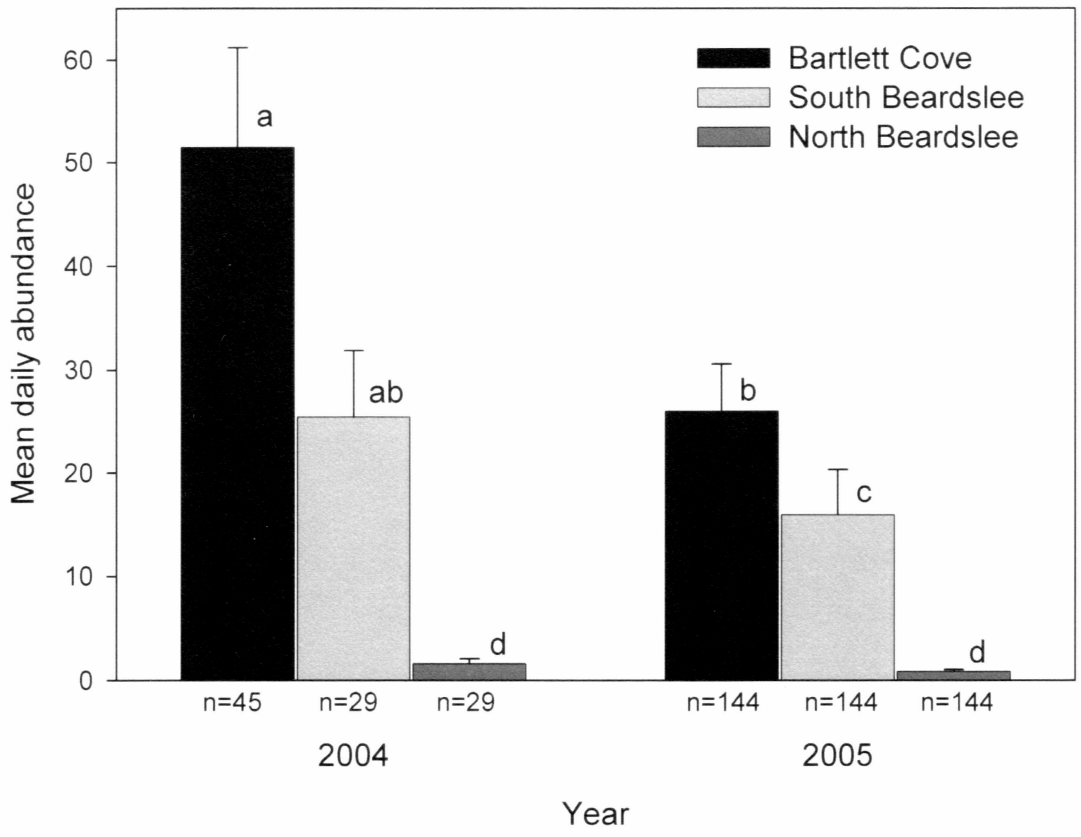

Fig. 2. *Cancer magister*. Mean daily megalopae abundance per light trap ± 1 SE for locations in Glacier Bay. Samples were collected in Bartlett Cove, the South Beardslee Islands and the North Beardslee Islands (inside) within 1 m of the surface in 2004 and 2005. Letters indicate significant differences at p = 0.05.

Table 2. Tukey-Kramer post hoc tests for *Cancer magister* megalopae abundance among years and locations.

Years	Locations	Probability	Significance
2004	BC and SB	0.3960	
	BC and NB	< 0.0001	***
	SB and NB	< 0.0001	***
2005	BC and SB	0.0002	*
	BC and NB	< 0.0001	***
	SB and NB	0.3970	
2004 and 2005	BC	< 0.0001	***
	SB	0.0004	*
	NB	0.3546	

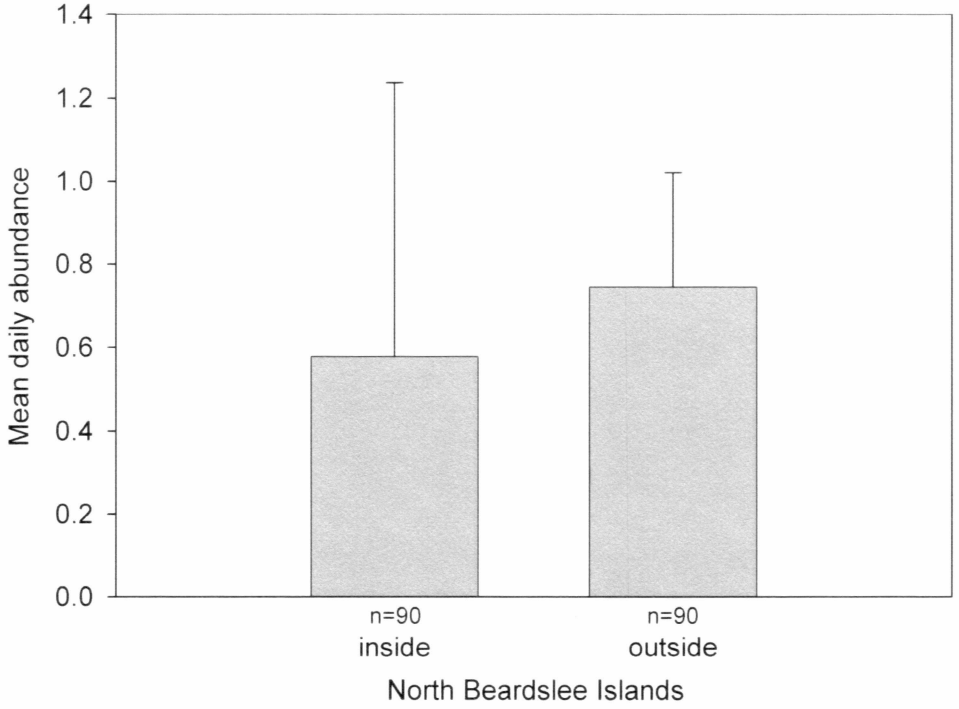

Fig. 3. *Cancer magister*. Mean daily megalopae abundance inside and outside North Beardslee Islands sites ± 1 SE. Samples were collected at the surface from October 5 – November 3, 2005. Differences in megalopae abundance between sites were not significant.

In 2005, over half of the megalopae at each site were collected over only two nights (Fig. 4). Two very large pulses of megalopae occurred at Bartlett Cove on October 3 (mean ± SE: 237.67 ± 80.40) and October 10 (mean ± SE: 249.67 ± 52.13). The two largest pulses in the South Beardslee Islands occurred on October 5 (mean ± SE: 293 ± 106) and October 21 (mean ± SE: 112 ± 60.53). The highest megalopae abundance in the North Beardslee Islands occurred on September 26 (mean ± SE: 10.67 ± 1.67 megalopae) and October 5 (mean ± SE: 10.67 ± 5.93 megalopae). These pulses represented 55.65 % of the total number of megalopae collected in Bartlett Cove, 52.9 % of the total number of megalopae collected in the South Beardslee Islands and 52.9 % of megalopae collected at the North Beardslee Islands. Megalopae abundance in Bartlett Cove was 36% higher in 2004 than in 2005.

Depth variation

Megalopae abundance was significantly higher in surface than in bottom traps at all sites (Fig. 5; Table 3). Surface traps captured 98.7% of the total megalopae collected in Bartlett Cove, 92.4% of the total megalopae collected in the South Beardslee Islands and 99.1% of megalopae in the North Beardslee Islands (Bartlett Cove $p < 0.0001$; South Beardslee Islands $p < 0.0001$; North Beardslee Islands $p < 0.0001$). The depth*location interaction was significant because surface samples from the North Beardslee Islands were not significantly different from bottom samples at Bartlett Cove ($p = 0.7928$) or the South Beardslee Islands ($p = 0.6153$).

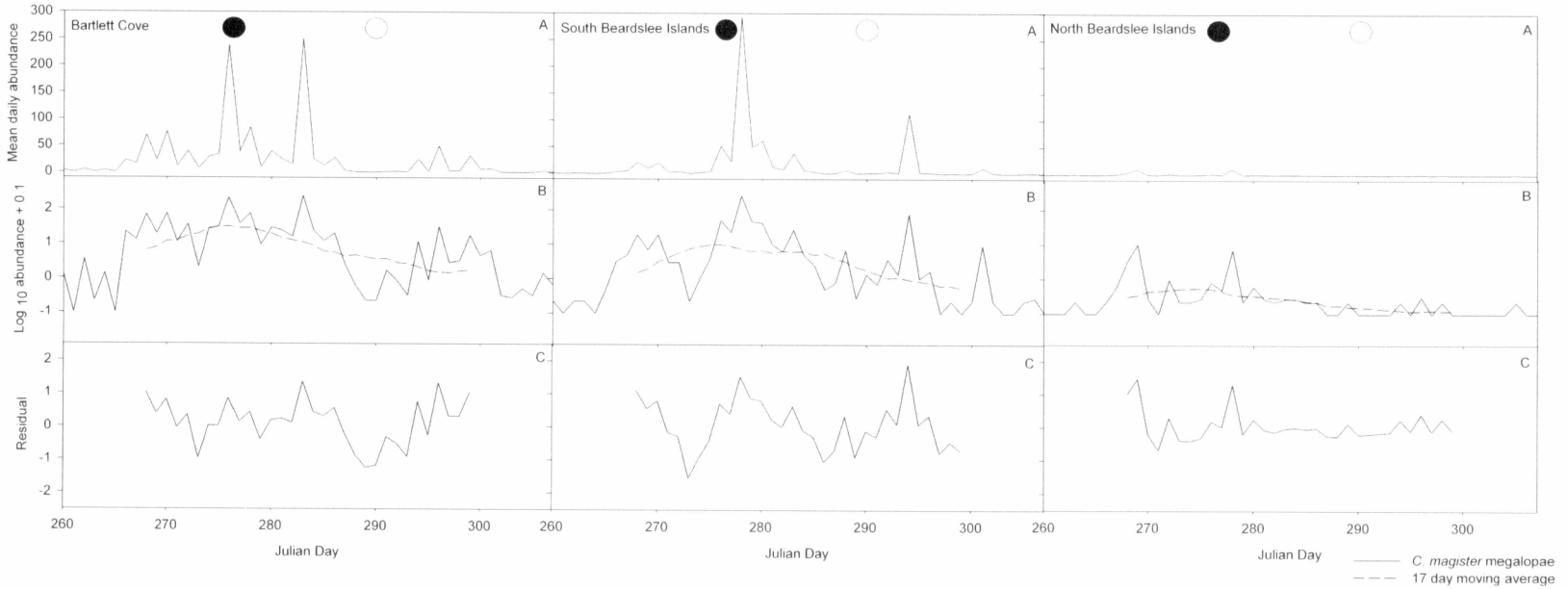

Fig. 4. *Cancer magister*. Megalopae abundances in surface light traps in Bartlett Cove, the South Beardslee Islands and the North Beardslee Islands (inside) from September 17 to November 3, 2005. (A) Average daily abundance. (B) Log_{10} (abundance + 0.1) indicated by a solid line and seasonal trend estimated by 17 day moving average indicated by a dashed line. (C) Residual between log transformed data and seasonal trend shown in panel (B).

Table 3. Summary of two-way GLM with effects location (Bartlett Cove, South Beardslee Islands or North Beardslee Islands) and depth (surface or bottom) upon log transformed daily *Cancer magister* megalopae abundance.

Source of variation	df	MS	F	Probability
Location	2	32.50	71.76	< 0.0001
Depth	1	158.55	350.02	< 0.0001
Location x Depth	2	12.30	27.16	< 0.0001
Error	423	0.45		

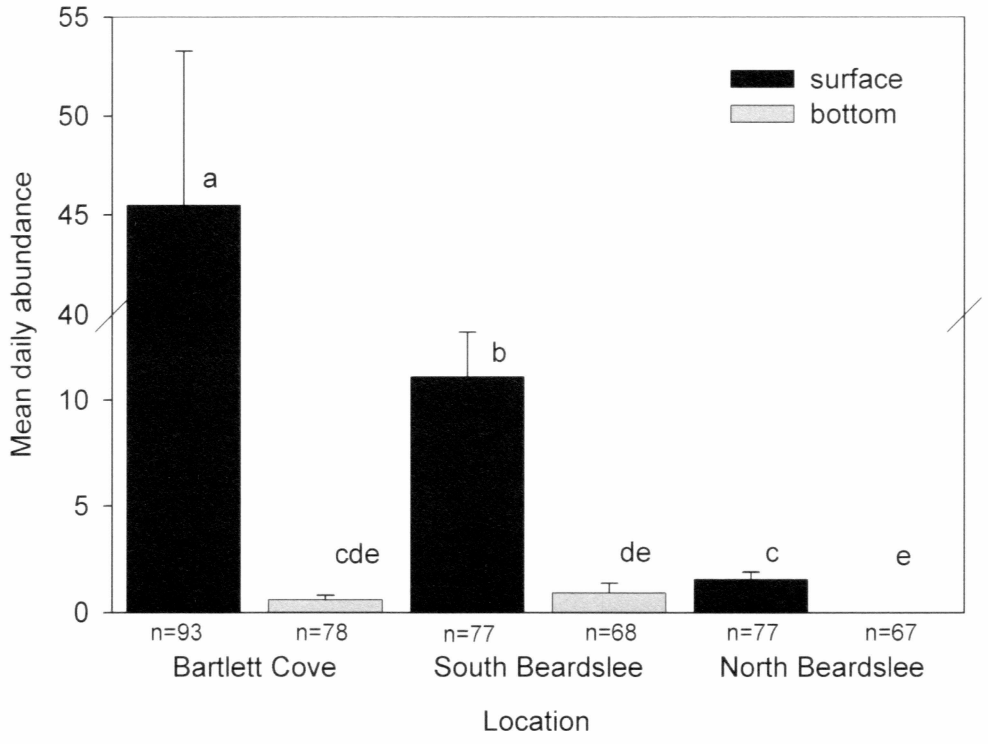

Fig. 5 *Cancer magister*. Mean daily megalopae abundances from light traps at the surface and at the bottom at 10 m depth (MLLW). Bottom samples were taken on a subset of simultaneous days for all sites in 2004 and 2005. Letters indicate significant differences among sites and depths at p = 0.05.

Pulse periodicity

Megalopae abundances were differently related to tidal amplitude and maximum wind speed among sites. Tidal amplitude was similarly correlated with megalopae abundance in the Beardslee Islands sites but was differently related with megalopae abundance in Bartlett Cove (Fig. 6, Table 4). Mean daily tidal amplitude

Table 4. Probabilities for cross-correlations of *Cancer magister* megalopae abundance with tidal amplitude and wind separated by location. Locations include Bartlett Cove (BC), the South Beardslee Islands (SB) and the North Beardslee Islands (NB). Lags represent days (only positive lags shown for correlations with maximum wind speed). Statistically significant results ($p < 0.05$) are shown in **bold**.

	Tidal amplitude			Wind speed		
Lag	BC	SB	NB	BC	SB	NB
-5	0.842	**0.002**	0.265	-	-	-
-4	0.392	**0.002**	0.207	-	-	-
-3	**0.020**	**0.012**	0.120	-	-	-
-2	**0.001**	0.146	0.117	-	-	-
-1	**0.000**	0.678	0.102	-	-	-
0	**0.000**	0.447	0.222	0.084	0.969	0.385
1	**0.017**	0.065	0.818	0.165	0.133	0.965
2	0.289	**0.013**	0.491	0.354	**0.013**	0.886
3	0.705	**0.012**	0.422	0.867	**0.026**	0.489
4	0.185	0.062	0.552	0.696	0.250	0.840
5	0.060	0.378	0.533	0.319	0.833	0.968

was 447.9 ± 18 cm (± SE) and ranged from 223 - 646 cm. Megalopae abundance in Bartlett Cove was negatively correlated with tidal amplitude at 0-2 d lags after tides (Fig. 7a). The only positive correlation between megalopae abundance and tidal amplitude in Bartlett Cove occurred 5 d after tides and was not statistically significant. Megalopae abundances in the South Beardslee Islands were greatest 2-3 d after high amplitude tides (Fig.7b). Tidal amplitude was not significantly correlated with megalopae abundance in the North Beardslee Islands.

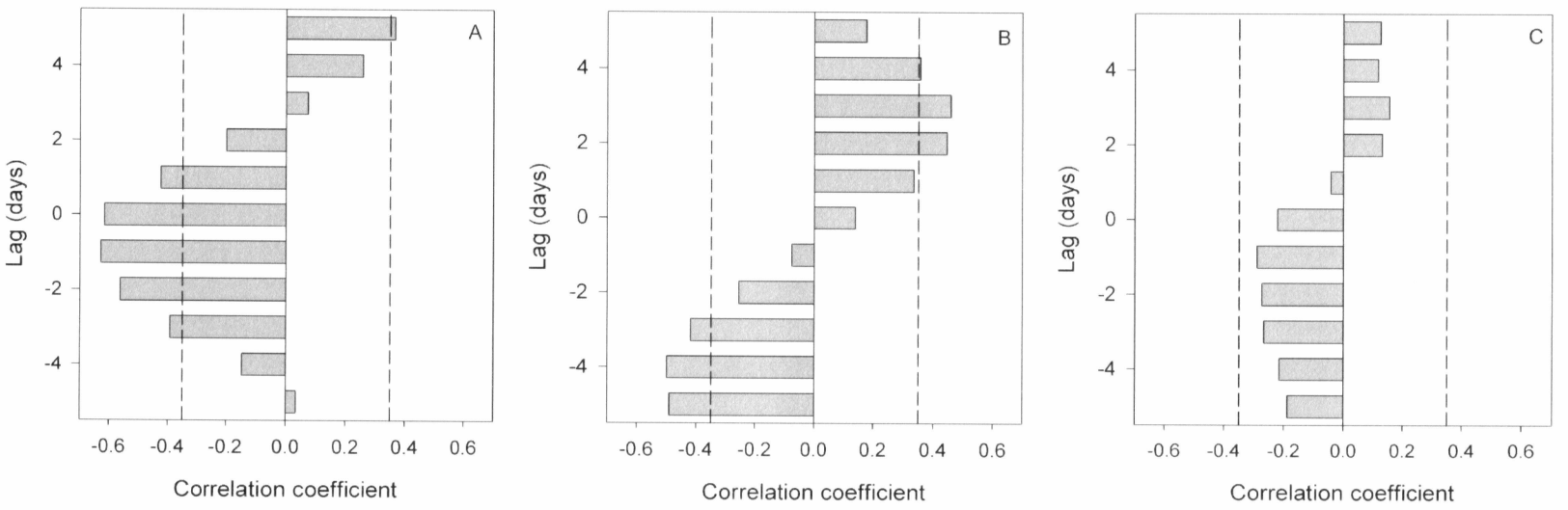

Fig. 6. Cross-correlations for *Cancer magister* megalopae abundance and tidal amplitude in lower Glacier Bay with ARIMA time series analysis. (A) Bartlett Cove (B) South Beardslee Islands (C) North Beardslee Islands. Positive lags represent tidal amplitudes before megalopae abundances. (A) Changes in megalopae abundance at Bartlett Cove were negatively correlated with tidal amplitude at -3 to +1 d lags. Megalopae abundance was positively correlated with tidal amplitude at +5 d lags. (B) Changes in megalopae abundance in the South Beardslee Islands occurred 2-3 d after changes in tidal amplitude. The lowest megalopae abundances occurred 4-5 d before high amplitude tides. (C) Megalopae abundance in the North Beardslee Islands was not significantly affected by tidal amplitude. Dashed lines represent 2 standard errors.

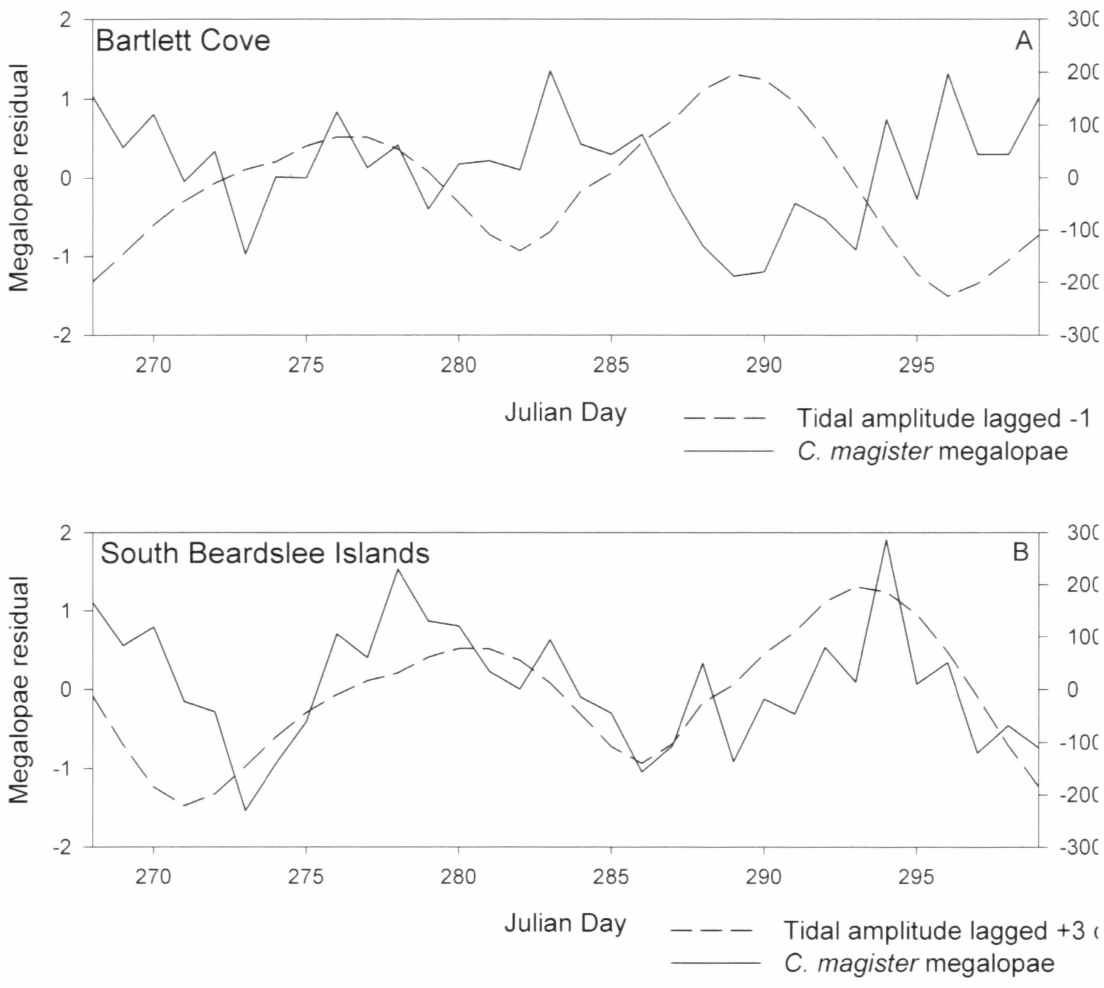

Fig. 7. Most significant cross-correlations between *Cancer magister* megalopae abundance (solid line) and tidal amplitude in cm (dashed line). (A) Negative correlation in Bartlett Cove with -1 d lag ($r = -0.628$, $p < 0.0001$). (B) Positive correlation in the South Beardslee Islands with + 3 d lag ($r = +0.459$, $p < 0.012$).

Megalopae abundances did not have any strong positive correlation with maximum wind speed (Fig. 8, Table 4). Maximum daily wind speeds ranged from 3.6 to 17.0 m s^{-1} over the sampling period with a mean daily wind speed of 6.8 ± 0.4 m s^{-1} (± SE). Changes in megalopae abundance in Bartlett Cove were positively correlated with changes in maximum wind speed at 0 d lags after winds; however,

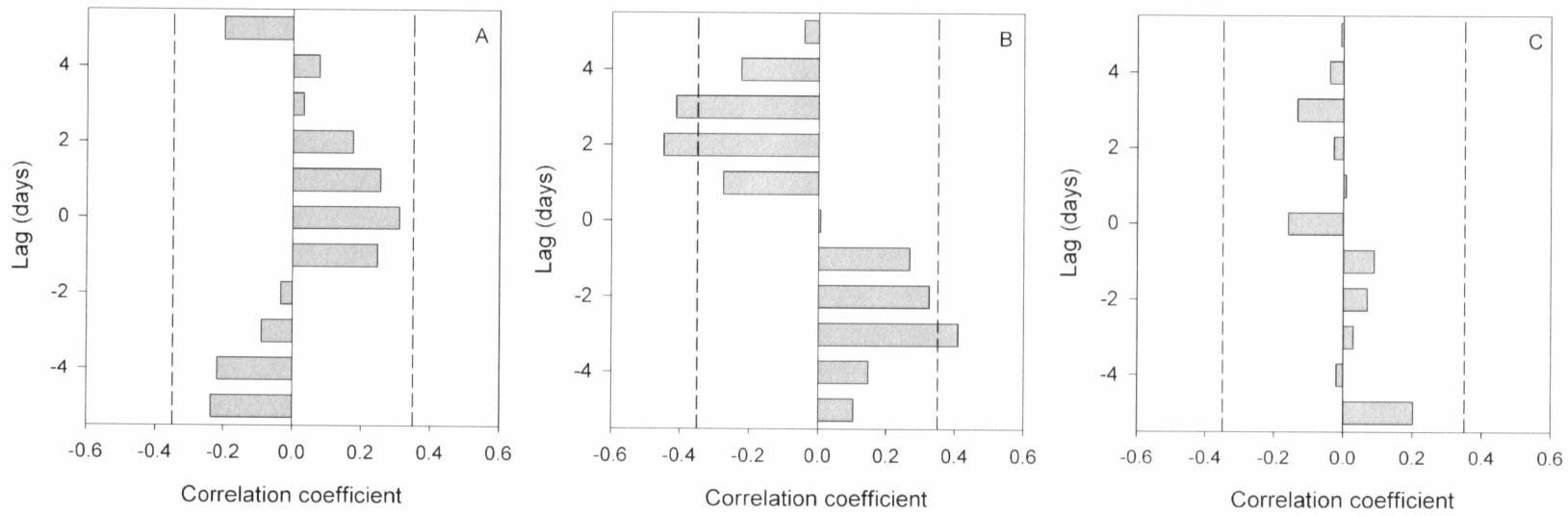

Fig. 8. Cross-correlations for *Cancer magister* megalopae abundance and maximum sustained wind speed in lower Glacier Bay with ARIMA time series analysis. (A) Bartlett Cove (B) South Beardslee Islands (C) North Beardslee Islands. Positive lags (days after winds) shown only. (A) Changes in megalopae abundance in Bartlett Cove were positively correlated with wind speed at a 0 d lag (B) Changes in megalopae abundance in the South Beardslee Islands were negatively correlated with wind speed at 2 to 3 d lags (C) Changes in megalopae abundance in the North Beardslee Islands showed no significant correlation with wind speed. Dashed lines represent 2 standard errors.

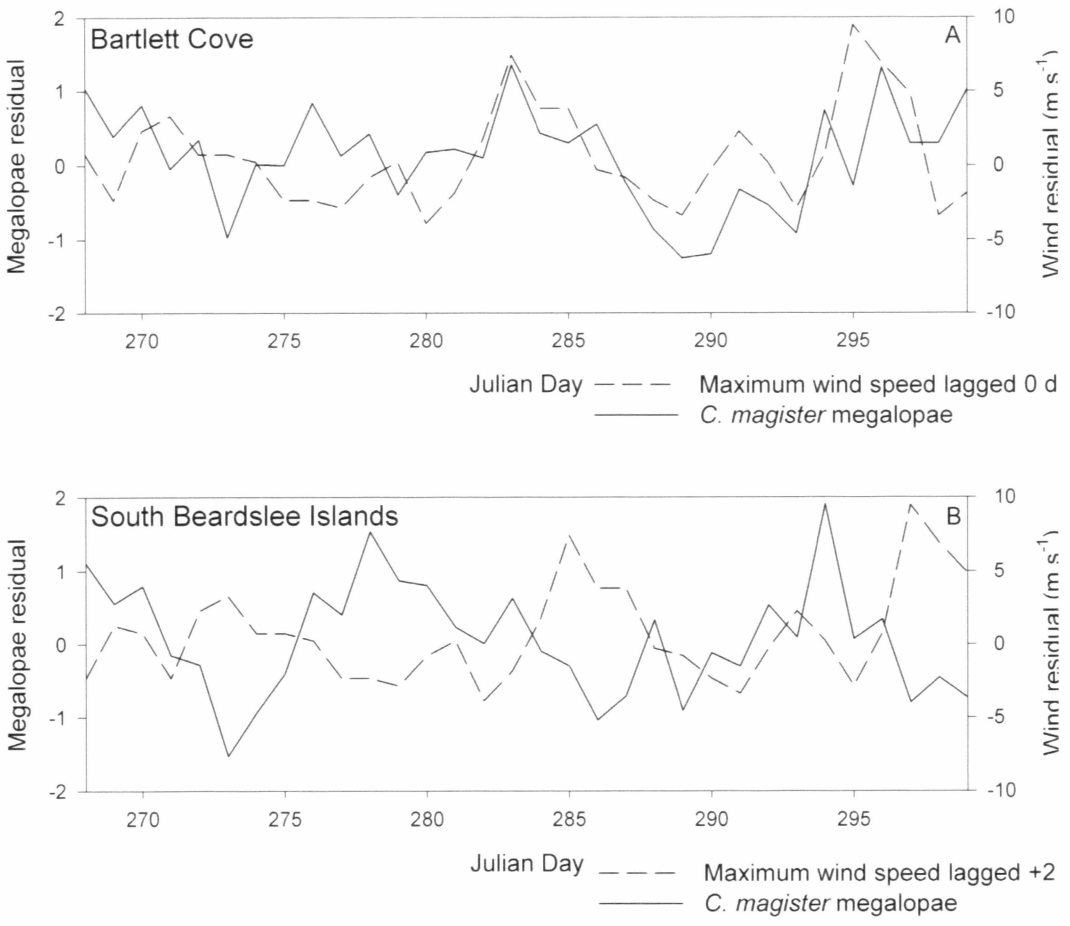

Fig. 9. Most significant cross-correlations between *Cancer magister* megalopae abundance (solid line) and maximum sustained wind speed (dashed line). (A) Bartlett Cove at a 0 d lag ($r = + 0.310$, $p = 0.083$). (B) South Beardslee Islands at a +2 d lag ($r = - 0.448$, $p = 0.013$).

this relationship was not statistically significant (Fig. 9a). No positive correlation existed between megalopae abundance and maximum sustained wind speed at positive lags in the Beardslee Islands, however a strong negative relationship existed between megalopae abundance in the South Beardslee Islands and wind speed lagged 2-3 d (Fig. 9b). Megalopae abundances were best correlated with non-directional

wind speed maximums (r = 0.310) or south (r = 0.318) and east (0.278) winds, which were the predominant directions of high winds during the sampling season (Fig. 10).

Non-transformed *C. magister* megalopae abundances were correlated within replicate surface traps at each site (BC r = 0.782 to 0.931; SB r = 0.844 to 0.905; NB r = 0.649 to 0.833).

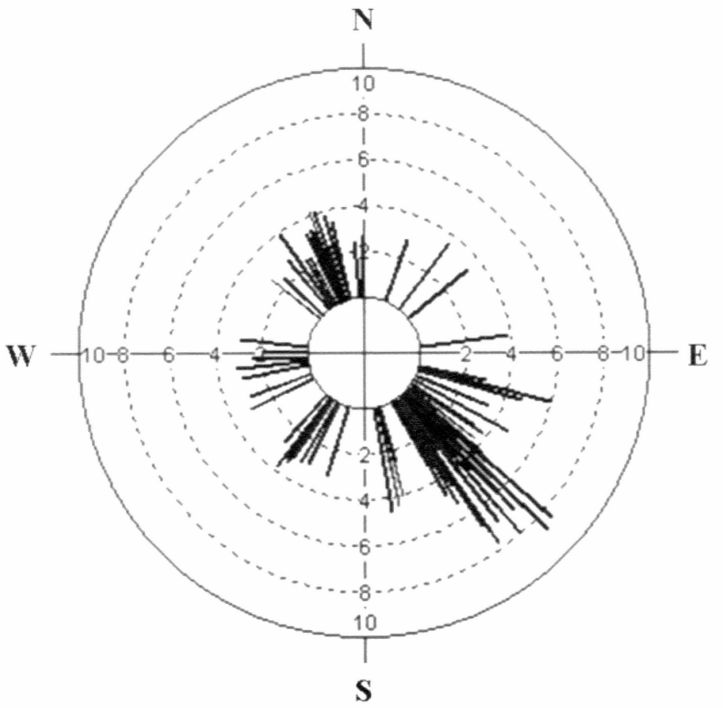

Fig. 10. Mean daily wind speed and direction in Gustavus, AK from September 10 to November 10, 2005. Degree angle indicates mean wind direction and length of bar indicates mean wind speed (m s^{-1}). Winds were predominately from the southeast during this time, especially high winds.

DISCUSSION

Spatial variation

Megalopae abundance varied significantly among sites sampled in this study and decreased with increasing distance from the mouth of Glacier Bay. Differences in megalopae abundance among sites were surprising considering that sites are only separated by 4-12 km and that all sites are similarly located on the east side of Glacier Bay and within the region of Glacier Bay with the highest adult crab abundances (Taggart et al. 2003). Megalopae were most abundant in Bartlett Cove, followed by South Beardslee Islands. Low megalopae abundances and no sizeable pulses of megalopae were observed in the North Beardslee Islands at sites both inside and outside of the island archipelago, suggesting that the this region has low densities of megalopae. The findings at both North Beardslee Islands sites confirm that these results are not a reflection of restricted water flow to that immediate area or some other localized effect. If megalopae invade Glacier Bay just prior to settlement, spatial variation in *C. magister* megalopae abundance in the lower portion of Glacier Bay may result from decreased megalopae supply with increased distance from the mouth of the Bay or from differences in transport processes supplying megalopae to localized areas (see below: *Pulse Periodicity*).

Differences in transport processes may affect the observed spatial variation in megalopae abundance between Bartlett Cove and the South Beardslee Islands through differences in local hydrodynamics, even when separated by small (< 10 km) distances. Existing knowledge of processes affecting larval transport may be used to

predict variations in larval supply or recruitment in fisheries management but it is usually more practical to retrospectively examine patterns of variation in time and space and infer dispersal pathways (Sale and Kritzer 2003). High spatial variability in larval recruitment of the bluehead wrasse (*Thalasoma bifasciatum*) occurred among sites separated by only a few km, where the greatest pulses in recruitment occurred on the leeward side of an island and were related to retention events (Swearer et al. 1999). Fewer larvae recruited on the windward side of the island, and these larvae came from somewhere else (Swearer et al. 1999). In our study, patterns of spatial variation in megalopae abundance were similar over annual and interannual time scales, suggesting that among-site variation in megalopae abundance may be consistent.

Upon entering Glacier Bay, megalopae encountering appropriate habitat in Bartlett Cove and the South Beardslee Islands may settle to the benthos, which would reduce the number of megalopae available for further up-bay transport. This process could result in the observed gradient of decreasing megalopae abundance with increasing distance from the mouth of the Bay. Blue crabs *(Callinectes sapidus)* have a similar life history pattern to Dungeness crabs in that their larvae are far-dispersing and make off-shore migrations (Epifanio et al. 1984, Johnson 1985, Epifanio & Garvine 2001). This species will be included in our discussion of transport processes as another brachyuran crab with a similar larval life history. Megalopae abundances for *C. sapidus* did not vary among locations in the lower, middle and upper portions of the North Inlet estuary in South Carolina (Christy & Morgan 1998). However,

settlement of *C. sapidus* megalopae in the York River, Chesapeake Bay was related to habitat availability and distance from the river mouth (Lipcius et al. 2005). Settlement was highest in seagrass beds which were only available near the mouth. Settlement was low in the middle portion of the bay but high once again at the site farthest up river. Lipcius et al. (2005) hypothesized that once megalopae entered the estuary, settlement would be dependent on the availability of preferred habitat. Once the seagrass habitat was saturated, megalopae would continue up river until they were at the edge of their salinity tolerance. There they would be forced to settle despite the lack of seagrass. Intertidal habitats are similar in Bartlett Cove and the Beardslee Islands and are composed largely of rock and mudflat bottoms (personal observation). Although habitat does not vary greatly along the gradient from Bartlett Cove to the North Beardslee Islands, habitat closer to the mouth of Glacier Bay may not be saturated and so megalopae may settle these areas in high abundances, reducing the availability of megalopae for further transport up bay.

An alternate hypothesis is that megalopae are adapted to settle near the mouths of estuaries as a way to avoid osmotic stress as juveniles. Higher settlement of *C. sapidus* megalopae near the mouth of Mobile Bay, Alabama was thought to reflect juvenile salinity tolerances (Morgan et al. 1996). First instar juvenile Dungeness crabs are also sensitive to reduced salinity environments (Brown & Terwilliger 1992) and these megalopae may too settle closer to the mouths of estuaries as a reflection of osmotic preference. The upper portion of Glacier Bay,

beyond the northern edge of the Beardslee Islands, has a persistent freshwater lens that may not be conducive to larval transport.

Depth variation

High abundances of megalopae were caught in surface traps but not in bottom traps, suggesting that megalopae may be aggregated in surface waters at night. When megalopae are present in surface waters they are available for transport by physical forcing mechanisms, such as tidal exchange or wind-driven surface currents (Epifanio 1988, McConaugha 1988). The presence of high abundances of megalopae at the surface suggests that *C. magister* megalopae are being transported at the time of this study and that transport processes may be behaviorally mediated. We offer three possible explanations of why bottom traps collected few megalopae, including: (1) megalopae maintain position in surface waters during all times of day and night, (2) megalopae are sometimes aggregated near the bottom but bottom light traps are ineffective (3) megalopae only aggregate in surface waters and are otherwise diffuse through the water column.

Because light traps are necessarily less effective during daylight hours, we can say very little about the location of megalopae during the day. Megalopae may well aggregate in surface waters during all times of the day and night. Behaviors maintaining *C. magister* megalopae near the surface have been observed at long distances from the coast (Reilly 1983) but not in estuarine areas. If megalopae in Glacier Bay were maintaining position near the surface during the day and night, megalopae caught in bottom traps may represent only late inter-molt stages preparing

for settlement. Megalopae were rarely caught in light traps positioned near the bottom but we are unable to relate these low abundances to vertical migration behaviors without higher resolution sampling. The possibility that megalopae remain in surface waters during all times of day and night seems unlikely because if megalopae always maintained their position near the surface they would be flushed in and out of Glacier Bay with each tidal exchange resulting in zero net transport up bay. Also, constant positioning in surface waters has not been previously observed for *C. magister* megalopae in estuarine areas.

Megalopae in Glacier Bay may otherwise make vertical migrations and only aggregate in surface waters at times. Diurnal vertical migration behavior has been shown for *C. magister* in other nearshore areas (Jamieson & Phillips 1988, Jamieson et al. 1989, Hobbs & Botsford 1992, Wing et al 1998). Vertical migrations may also be tidally timed. This behavior has not been observed for *C. magister* megalopae but has been well studied for *C. sapidus* (Brookins & Epifanio 1985, Mense & Wenner 1989, Little & Epifanio 1991, DeVries et al. 1994).

If megalopae time their migration into surface waters to facilitate up-bay transport they may at other times be aggregated near the bottom so as to retain their position. If megalopae are at times aggregated near the bottom, the ineffectiveness of bottom light traps may have been due to the light level or to trap positioning. Light from bottom traps may appear to be more diffuse during the day and less attractive to megalopae in the vicinity. Many brachyuran megalopae of estuarine species are positively attracted to point sources of light, but they will swim away from areas of

diffuse light (Forward 1987b). Alternatively, megalopae may have been present at the direct interface with the benthic substrate rather than at 1 m above the bottom where our traps were positioned. Depth-stratified plankton tows in Bartlett Cove during the day rarely caught megalopae at any depth; however the tows generally remained several meters above the bottom (Fisher 2005). Megalopae were caught once in a plankton tow which hit the ocean floor and brought up substrate (J. Fisher personal communication). Megalopae in Glacier Bay may be located in the substrate to retain their position when they are not in surface waters. Such behavior may be especially necessary in highly turbulent areas of Glacier Bay with strong tidal currents where controlling vertical positioning could be difficult. If this is the case, our light traps at approximately 1 m from the bottom may have simply been too far removed from the substrate to encounter megalopae.

Megalopae may otherwise not be aggregated unless they are at the surface. *Cancer magister* megalopae off the coast of Vancouver Island aggregate in surface waters at night and are otherwise diffuse throughout the top 15 m of the water column (Jamieson et al. 1989). Vertical migration behaviors of *C. sapidus* are both tidal and diurnal as megalopae are less aggregated and found deeper within the water column with increased ambient light (Olmi 1994). If megalopae do not aggregate unless they are in surface waters, megalopae would not be caught in abundance by sampling only one additional depth.

Pulse Periodicity

Pulses of high megalopae abundance were temporally distinct among locations and may be attributed to differences in hydrodynamics and transport processes. High megalopae abundances occurred in Bartlett Cove during neap tidal periods; however, megalopae abundances in the South Beardslee Islands were highest a few days after maximum tidal amplitudes during both new and full moon stages. High *C. magister* and *C. sapidus* megalopae abundances have been related to most tidal stages. Peaks in *C. magister* or *C. sapidus* settler abundance have been related to both neap tides near half or quarter moons (Boylan & Wenner 1993, Johnson & Shanks 2002, Miller & Shanks 2004) and to spring tides near new and full moons (Mense et al. 1995, Miller & Shanks 2004). Temporal variation in *C. magister* megalopae recruitment has also been observed between areas separated by less than 10 km in Grays Harbor and Willapa Bay with weak to no correlation in megalopae abundance between sites (Roegner et al. 2003).

Megalopae abundances were positively correlated with maximum wind speed at a 0 d lag in Bartlett Cove but not at any of the other sites. The correlation with wind speed was less significant than were correlations with tidal amplitude but may be biologically significant. Episodic high wind events may affect megalopae transport to nearshore areas periodically as an additive effect when other conditions (e.g. lunar and tidal cycles) are such that high abundances of megalopae would be expected. Or, megalopae transport by wind may only be related to periods of high sustained wind speeds, such as storm events, and not necessarily with daily wind

speeds throughout the settlement season. Occurrences of high megalopae abundance associated with periods of high wind have primarily been linked to upwelling events (Miller & Shanks 2004), but storm events also affect dispersal and spatial distribution of megalopae (McConnaughey et al. 1992, Etherington & Eggleston 2000). Megalopae abundances were best correlated with winds from the southeast but the effect of wind direction on megalopae supply is difficult to determine as storm events typically arrive from the southeast and this was the predominant direction of high speed winds during the sampling season. Glacier Bay is known for high wind activity and storm events, especially during fall months when recruitment of *C. magister* megalopae occurs and wind should not be discounted as a potential mechanism of megalopae supply or spatial variation among locations. Wind forcing may also contribute to spatial variation in megalopae abundances, as has been previously observed in Grey's Harbor (Eggleston & Armstrong 1995).

Megalopae abundances in the South Beardslee Islands were negatively correlated with wind speed at +2 to +3 d lags. The correlation with wind at this lag is the same as the correlation between abundance and tidal amplitude suggesting that these causal variables may have been confounded. The settlement season for *C. magister* in this area, and therefore the length of our time series, is relatively short and so correlations are more substantially affected by chance events. The two major storm events, which corresponded with pulses of high megalopae abundance in Bartlett Cove, occurred on October 10 (maximum sustained: 8.2 – 12.9 m s^{-1}) and October 23 – 25 (maximum sustained: 10.8 – 14.9 m s^{-1}) which were approximately

14 days apart. By chance, the periodicity of these major 2005 wind events corresponded with a tidal periodicity which may confound cross-correlations. This is apparent in the negative relationship between megalopae abundance and wind speed in the South Beardslee Islands.

Megalopae abundances in the South Beardslee Islands seem to be governed only by tidal transport whereas wind transport and behaviors based on lunar periodicities also seem to play a role in megalopae supply to Bartlett Cove. We offer two possible explanations as to why tidal transport may more substantially affect megalopae transport to the South Beardslee Islands than to Bartlett Cove. The first scenario, is that megalopae from the mouth of Glacier Bay are funneled into Bartlett Cove and travel into the South Beardslee Islands through a transitory "backdoor" waterway at the head of Bartlett Cove. This waterway is dry during most low tides and is only navigable by small crafts at tidal heights greater than 2.5 m. More water is available in this waterway for longer periods of time during high amplitude tides and could result in pulses of megalopae being washed through to the South Beardslee Islands at those times. In this scenario, the low megalopae abundances observed in the North Beardslee Islands might be explained by the low abundances of larvae that make it through the transitory waterway and are flushed northward.

It is more likely that megalopae are transported to the South Beardslee Islands through the main waterway from the mouth of Glacier Bay, Sitakaday Narrows. If this is the case, megalopae transported through the highly turbulent Sitakaday Narrows probably are less able to control their vertical position than megalopae

entering Bartlett Cove which may result in different pulse periodicities between these two sites. If megalopae are transported into the South Beardslee Islands through the main waterway, they would have to go through Sitakaday Narrows, a shallow (50 m) and narrow (4-8 km) sill where the entire water column is mixed four times daily during maximum ebb and flood tides (Hooge & Hooge 2002). Average tidal currents in Sitakaday Narrows measure 2.6 and 2.7 m/s during ebb and flood tides, respectively, with maximum current speeds at 4.5 m/s (Hooge et al. 2000, Hooge & Hooge 2002). In nearly every oceanographic survey from 1992 to 2000, the water column was fully mixed in at least one CTD cast in the lower part of Glacier Bay. Surface waters during maximum ebb or flood tide were described as "a highly turbulent fast-flowing river, with standing waves, whirlpools and roils" (Hooge & Hooge 2002). In this extreme environment, megalopae may not be able to control vertical positioning, especially during high amplitude tides. Megalopae at the entrance to Bartlett Cove may make vertical migrations to utilize surface transport processes and such as selective tidal stream transport (STST) while megalopae at the entrance to the South Beardslee Islands are simply washed in with tidal exchanges.

Selective tidal stream transport has not been shown explicitly for Dungeness crab larvae but has been well studied in *C. sapidus* larvae. Selective tidal stream transport allows crab megalopae to exploit tidally driven estuarine flow for up-bay transport by controlling their vertical position within the water column through swimming behaviors and enter surface waters during nocturnal rising tides (Brookins & Epifanio 1985, Mense & Wenner 1989, Little & Epifanio 1991, DeVries et al.

1994). This mechanism has been well documented as a mechanism for *C. sapidus* megalopae migrations back into estuarine areas after development on the continental shelf (Epifanio & Garvine 2001, Forward et al. 2003). *Cancer magister* megalopae are excellent swimmers with swimming speeds ranging from 8.5 cm s^{-1} in still water to 44.8 cm s^{-1} against current speeds of 40 cm s^{-1} (Fernandez et al. 1994). These speeds are faster than the maximum swimming speeds of *C. sapidus* at 20 cm s^{-1} (Luckenbach & Orth 1992) and should therefore allow sufficient control over vertical positioning within the water column to utilize STST for up-estuary transport. At long distances from the coast *C. magister* megalopae are found in highest abundances within 15 m of the surface during the day and night (Reilly 1983); however, as megalopae move closer to shore they begin to make diurnal vertical migrations in which they are only at the surface during night time hours, sometimes having peaks near dusk and dawn (Jamieson & Phillips 1988, Jamieson et al. 1989, Hobbs & Botsford 1992, Wing et al 1998).

Megalopae might use selective tidal stream transport to enter Bartlett Cove but be simply washed into the South Beardslee Islands with tidal exchanges. The entrance to Bartlett Cove is a less extreme environment where vertical positioning would be easier for megalopae to control than in Sitakaday Narrows. This hypothetical difference in transport processes could result in the observed spatial variation in megalopae abundance with Bartlett Cove receiving significantly more megalopae by STST than the Beardslee Islands. Selective tidal stream transport may be an effective mechanism for entry into Bartlett Cove during low amplitude tides but

break down during high amplitude tides when mixing and turbulence is increased. Such a breakdown in STST at the mouth of Bartlett Cove during spring tides would result in the observed negative relationship between tidal amplitude and megalopae abundance at that location. In Sitakaday Narrows, STST is likely to break down regardless of tidal amplitude. Without the ability to utilize STST, megalopae at the entrance to Sitakaday Narrows would be swept through to the South Beardslee Islands with high amplitude tides resulting in the strong correlation between megalopae abundance and tidal amplitude at this site. Without STST, transport would not continue with subsequent tidal cycles beyond Sitakaday Narrows and very few megalopae would progress further up bay. This hypothetical breakdown in transport processes may result in the observed low abundances of *C. magister* megalopae in the North Beardslee Islands.

Marine reserve connectivity and sustainability

Identification of areas important to early life stages and maximization of connectivity between reserves and outside areas via larval and adult dispersal are priorities in marine reserve design (Jones 2002, Roberts et al. 2003a, b, Botsford et al. 2003). However, marine reserves are usually created opportunistically with little scientific effort put into the identification of such areas (Carr & Reed 1993, Allison et al. 1998, Russ 2002). Theoretical studies have primarily focused on unidirectional transport from within a reserve to outside areas as a means of improving fisheries yields (Guénette et al. 1998, Gell & Roberts 2003, Lubchenco et al. 2003, Gaylord et al. 2005). The potential for dispersing larvae to improve fisheries yields remains a

highly controversial subject with arguments both in support of (Roberts et al. 2001, Tegner 1992) and against (Willis et al. 2003, Hilborn et al. 2006) the functionality of marine reserves as applied to fisheries management. The potential effects of larval recruitment in marine reserves from larvae transported in from other areas have not been discussed.

Dungeness crab larvae may be exported from Glacier Bay in early zoeal stages (Fisher 2005) and so have a "seeding" effect on populations outside of the reserve. However, recruitment of larvae back to the reserve is necessary to ensure the sustainability and conservation of the population (Botsford et al. 1998, Botsford et al. 2001, Gaines et al. 2003, Hastings & Botsford 2006). In this study we have argued for transport of Dungeness crab megalopae into Glacier Bay just prior to settlement which suggests notable connectivity in both directions between the reserve and outside areas. Probably, larvae exported from Glacier Bay mix with those from outside areas and become part of some metapopulation, a portion of which are transported into Glacier Bay as megalopae. Mean measurements of larval dispersal distance are difficult to obtain but needed to design or determine marine reserves as self-recruiting (Palumbi 2003, 2004, Sotka & Palumbi 2006). If Dungeness crabs in Glacier Bay are not self-recruiting then the health and abundance of crabs in outside populations would play a role in the sustainability of the reserve population. Larval supply to Glacier Bay may therefore depend more on the abundance of crabs in the greater metapopulation, rather than the abundance of crabs in Glacier Bay. That is, marine reserve status does not necessarily affect a higher abundance of new recruits

to the Dungeness crab population in Glacier Bay. In the case where larvae are exported from marine reserves, a network of reserves spaced so that larvae produced by a population in one reserve replenishes the population in other reserves may be a better design in terms of species conservation and marine reserve sustainability (Shanks et al. 2003).

CONCLUSION

Substantial spatial variation exists in *Cancer magister* megalopae abundances in the lower portion of Glacier Bay. Such spatial variation is thought to result from differences in hydrodynamic transport processes as megalopae are transported into Glacier Bay from outside areas. Megalopae abundances decreased with increasing distance from the mouth of Glacier Bay. Pulses of high megalopae abundance vary temporally among locations and are differently correlated with tidal amplitude and maximum sustained wind speeds among locations. When considering the implications of this marine reserve in relation to management of the Dungeness crab fishery, it is important to acknowledge that although larvae from Glacier Bay may disperse to outside areas and seed the fished population, the sustainability of Glacier Bay as a marine reserve is also likely to be dependent on larvae supplied from areas outside of Glacier Bay.

SUGGESTION FOR FUTURE RESEARCH

Observations of variation in megalopae abundance, in concert with a limited understanding of the physical oceanography in Glacier Bay, suggest that megalopae supply may explain the spatial pattern of adult crab abundance. Adult abundances drop abruptly just beyond the northern edge of the Beardslee Islands at the Sitakaday Narrows shelf break, and no abiotic factor has been identified that would be limiting to adult abundances in this region (Taggart et al. 2003). Spatial variations in late stage larvae of snow crab (*Chionoecetes opilio*) and pandalid shrimp (*Pandalus montagui*) were related to variations in adult abundances at two sites in a western Canadian fjord that varied by only a few km (Quijon & Snelgrove 2005). In this case, spatial variation in larvae supply influenced adult distributions, because of limitations of larval transport and adult dispersal across a shallow sill. If tidally driven transport processes break down in Sitakaday Narrows, adult abundances in the upper portion of Glacier Bay may be limited by low megalopae supply. The waters beyond the Sitakaday Narrows shelf Glacier Bay are highly stratified with a persistent freshwater lens and constant surface outflow even during flood tides (Hooge & Hooge 2002) which could additionally complicate megalopae transport farther up-bay. Without STST, megalopae supply to the upper bay would be limited but may occur periodically such as during storm events, explaining the relatively low density of adult crabs in that area.

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APPENDIX

Sampling dates with number of replicates

	2004						2005						
	surface			bottom			surface				bottom		
Date	BC	SB	NB inside	BC	SB	NB inside	BC	SB	NB inside	NB outside	BC	SB	NB inside
11-Sep	2	0	0	2	0	0							
12-Sep	3	0	0	2	0	0							
13-Sep	3	0	0	2	0	0							
14-Sep	3	0	0	3	0	0							
15-Sep	3	0	0	3	0	0							
16-Sep	3	0	0	3	0	0							
17-Sep	3	3	0	3	3	0	3	3	3	0	3	3	3
18-Sep	3	3	0	3	3	0	3	3	3	0	3	3	3
19-Sep	3	2	3	3	2	3	3	3	3	0	3	3	3
20-Sep	3	2	3	3	2	3	3	3	3	0	3	3	3
21-Sep	3	0	3	3	0	3	3	3	3	0	3	3	3
22-Sep	2	0	0	3	0	0	3	3	3	0	3	3	3
23-Sep	3	0	0	3	0	0	3	3	3	0	3	3	3
24-Sep	2	0	0	2	0	0	3	3	3	0	3	3	3
25-Sep	2	0	0	2	0	0	3	3	3	0	3	3	3
26-Sep	0	0	0	0	0	0	3	3	3	0	3	3	3
27-Sep	0	0	0	0	0	0	3	3	3	0	3	3	3
28-Sep	3	0	0	3	0	0	3	3	3	0	3	3	3
29-Sep	3	0	0	3	0	0	3	3	3	0	3	2	3
30-Sep	3	0	0	3	0	0	3	3	3	0	3	3	3
1-Oct	2	0	0	3	2	0	3	3	3	0	3	3	3
2-Oct	3	1	0	3	2	0	3	3	3	0	3	3	3
3-Oct	0	0	0	0	0	0	3	3	3	0	3	3	3
4-Oct	0	0	0	0	0	0	3	3	3	0	3	3	3
5-Oct	0	0	0	0	0	0	3	3	3	3	0	3	3
6-Oct	0	0	0	0	0	0	3	3	3	3	0	3	3
7-Oct	3	0	0	2	0	0	3	3	3	3	0	3	3
8-Oct	3	0	0	3	0	0	3	3	3	3	0	3	3
9-Oct	3	0	0	3	0	0	3	3	3	3	0	3	3
10-Oct	3	1	3	3	1	3	3	3	3	3	0	3	3
11-Oct	3	1	3	3	2	3	3	3	3	3	0	3	3
12-Oct	3	2	3	3	2	3	3	3	3	3	0	3	3
13-Oct	3	2	3	3	2	3	3	3	3	3	0	3	3
14-Oct	3	2	3	3	2	2	3	3	3	3	0	3	3
15-Oct	3	3	3	3	2	2	3	3	3	3	0	3	3
16-Oct	3	3	3	3	3	2	3	3	3	3	0	3	3
17-Oct	3	2	3	3	3	2	3	3	3	3	0	3	3
18-Oct	3	2	2	2	2	2	3	3	3	3	0	3	3
19-Oct	3	2	2	2	2	2	3	3	3	3	0	0	0

	2004						2005						
	surface			bottom			surface				bottom		
Date	BC	SB	NB inside	BC	SB	NB inside	BC	SB	NB inside	NB outside	BC	SB	NB inside
20-Oct	3	0	0	3	0	0	3	3	3	3	0	0	0
21-Oct	3	0	0	3	0	0	3	3	3	3	0	0	0
22-Oct	3	0	0	3	0	0	3	3	3	3	0	0	0
23-Oct	3	0	0	3	0	0	3	3	3	3	0	0	0
24-Oct							3	3	3	3	0	0	0
25-Oct							3	3	3	3	0	0	0
26-Oct							3	3	3	3	0	0	0
27-Oct							3	3	3	3	0	0	0
28-Oct							3	3	3	3	0	0	0
29-Oct							3	3	3	3	0	0	0
30-Oct							3	3	3	3	0	0	0
31-Oct							3	3	3	3	0	0	0
1-Nov							3	3	3	3	0	0	0
2-Nov							3	3	3	3	0	0	0